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Ontario Hydro, Research Division
800 Kipling Avenue,
Toronto, Ontario, Canada
M8Z 5S4

Telex: 06-984-525

Phone: (416)231-4111

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ALLELOPATHY - THE EFFECT OF ONE SPECIES OF PLANT OR MICROORGANISM ON THE GROWTH AND DEVELOPMENT OF ANOTHER: A LITERATURE REVIEW

Report No 82-461-K

G.P. Arron
Biologist
Biological Research Section
Chemical Research Department

ABSTRACT

Many species of allelopathic plants and microorganisms have been identified which inhibit or stimulate the germination, growth or development of plants and microorganisms of the same or other species. These allelopathic effects are produced by the introduction (by a variety of means) of chemical compounds into the environment, and are thus separate from competition, which involves the removal or reduction of some factor from the environment that is required by some other organism sharing the habitat. The chemical compounds produced are usually secondary metabolites and influence many aspects of organism metabolism, including cell division, ion uptake, photosynthesis and respiration. Although allelopathy undoubtedly has a fundamental role in ecological succession in most ecosystems, such a role has been succinctly demonstrated in aquatic and grassland ecosystems only. Allelopathy has already been exploited in agriculture, where crop plants such as oats have been shown to have an allelopathic effect on weed growth and in reforestation programs where allelopathic tree species also reduce weed growth.

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740634-592-031	834.1	November 26, 1982	82-461-K

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EXECUTIVE SUMMARY

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G.P. Arron
Biologist
Biological Research Section
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Many plants and microorganisms exhibit allelopathic properties in that they produce chemical compounds which inhibit or stimulate the germination, growth or development of other species of plant or microorganism. Plants or microorganisms of one species can affect organisms of the same species or any other species (eg a tree can inhibit the growth of an herbaceous plant and vice versa).

Allelopathic effects are dependent upon the addition of a chemical compound to the environment, and are thus separate from competition which involves the removal or reduction of some factor from the environment that is required by some other plant sharing the habitat.

Allelopathic agents are produced by or are present in many different plant parts, eg, the leaves, stems, roots, fruits and seeds of higher plants. These agents are dispensed into the environment as emanates from leaves, leachates from leaves, exudates from roots, and upon the death of the plant during decay.

The vast majority of allelopathic agents are secondary metabolites since they have no recognized role in the maintenance of fundamental life processes in the organisms that synthesize them. Secondary metabolites with allelopathic properties exhibit great diversity in terms of chemical structure and have been classified into 14 major groups. Most of these metabolites are synthesized via the acetate or the shikimic acid pathways.

Many aspects of plant metabolism are affected by allelopathic agents including: cell division, hormone-induced growth, membrane permeability, ion uptake (apparently mediated by a direct effect on the membrane-bound plasma membrane ATPase), photosynthesis, respiration, protein synthesis, the activity of specific enzymes, and water relations.

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The role of allelopathy in manipulated ecosystems has been studied primarily in the agricultural area (for economic reasons), and in this and the reforestation area it may soon be possible to reduce the use of herbicides to control competing weed species as a direct result. Although it is known that allelopathy has a fundamental role in ecological succession, such a role has been effectively demonstrated in aquatic and grassland ecosystems only.

The role of allelopathy in vegetation control on rights-of-way operated by Ontario Hydro may be limited.

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To Mr. F.J. Kee
Director of Research

ALLELOPATHY - THE EFFECT OF ONE SPECIES OF PLANT OR MICROORGANISM ON THE GROWTH AND DEVELOPMENT OF ANOTHER: A LITERATURE REVIEW

1.0 INTRODUCTION

In order to ensure economical and reliable power transmission, Ontario Hydro uses various vegetation control techniques to produce communities of low-growing, persistent plant species on rights-of-way. The techniques employed include mechanical cutting, chemical control (herbicide application to various plant parts, eg, stem and foliage, the base of the plant, or the cut stump) and the infrequently used biological control (cover cropping). Because of a paucity of information on the effectiveness of these techniques in any given situation, it remains difficult to predict which individual technique (or combination) will be the most effective in the production of a desirable plant community on any particular right-of-way, since no two sections of right-of-way will be the same in an environmental sense (soil type, climate will be different). The effectiveness of any vegetation control strategy may be judged, at least in part, by the length of time between treatments. In the case of mechanical cutting and herbicide application, this can be from 5 to 6 years.

Adoption of a biological control technique may result in a cycle period far longer than this, with concomitant economic advantages. Although the introduction of allelopathic plant species onto rights-of-way would constitute such a biological control strategy, it has received scant attention in the literature.

The term allelopathy was coined by Molisch (1937) and has been repeatedly defined and redefined (Putnam and Duke, 1978). In current use (see Rice, 1974, 1979) the term refers to the detrimental effects of higher plants of one species on the germination, growth or development of plants of another species. Rice (1979) has pointed out that Molisch (1937) meant the term to cover both detrimental and beneficial reciprocal biochemical interactions, but there has been a tendency to eliminate the beneficial effects from the definition of late (Rice, 1974). This report will concentrate on the detrimental effects of allelopathy; there have been but few reports on the beneficial effects. The choice of the term by Molisch (1937) was perhaps technically erroneous in that allelopathy was derived from two Greek words meaning "mutual harm" (Rice, 1974). It should be noted that allelopathy is not only exhibited in higher plants, but algae and microorganisms also. An

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important point concerning allelopathy is that its effect is dependent upon the addition of a chemical compound to the environment, and it can thus be separated from competition which involves the removal or reduction of some factor from the environment that is required by some other plant (organism) sharing the habitat (Rice, 1979). Factors that may be reduced include water, minerals and light. Research efforts to document the existence of allelopathy in various ecosystems have been hampered by a lack of reliable techniques to separate allelopathic influences from other aspects of plant interference (Rice, 1979). Szczepanski (1977) recently described three possible mechanisms for plant interference, which include competition for necessary growth factors (allelospoly) (Bykov, 1970), addition of toxic factors to the environment (allelopathy), and possession of herbivore toxicant or repellant substances that prevent grazing (allelomediation).

Although allelopathy may involve one species of microorganism producing a chemical inhibitor effective against another species of microorganism, or a higher plant species, vying with a microorganism (with either in the role of chemical producer), this review will concentrate on the case where higher plants (in particular herbaceous and woody species) fill both roles.

2.0 ALLELOPATHIC EFFECTS

2.1 Allelopathic Effects of Plants on Other Plants or Microorganisms

DeCandolle (1832) was one of the first to suggest that some plants may excrete something from their roots which is injurious to other plants. No research activity occurred in this field until Schreiner and co-workers reported the production of toxins by crop plants which inhibited the same and other crop plants (Schreiner and Reed, 1907; Schreiner and Sullivan, 1909). McCalla and Duley (1948, 1949) described how decaying wheat residues or extracts of sweet clover reduced the germination and growth of corn. Many papers were published in the next 25 years concerning allelopathic effects of crop plants on other crop plants. Among the crop plants reported to be inhibitory were barley (Overland, 1966), red clover (Tamura et al, 1969), prairie sunflower (Curtis and Cottam, 1950), timothy, corn, rye and tobacco (Patrick and Koch, 1958) and oat (Rakhteenko et al, 1973).

The crop plants mentioned above will only inhibit certain other crop plants - there is some degree of specificity. Zabyalyendzik (1973) showed this in this study of the mutual interactions of buckwheat (*Fagopyrum*), lupine (*Lupinus*), mustard (*Brassica*) and oats (*Avena sativa*) in field and greenhouse experiments. Water soluble root exudates of lupine and mustard stimulated growth and development of buckwheat. Water soluble exudates of oats, however, inhibited growth and yield of buckwheat. Root exudates of buckwheat stimulated growth of oats increasing its productivity 10 to 20% in comparison with controls, whereas exudates of buckwheat inhibited growth and yield of lupine. These allelopathic effects (and those described below) are presented in simplified form in Table 1 for an easier comparison of the various sources of allelopathic agent and effects observed.

Table 1. Summary of some reported allelopathic effects of crop plants and weeds on other plants

Plant Producing Allelopathic Agent	Source of Agent	Plant Affected	Effect
Wheat	Decaying residues	Corn	-
Sweet clover	Extract of	Corn	-
Buckwheat	Root exudate	Oats	+
Buckwheat	Root exudate	Lupine	-
Lupine	Root exudate	Buckwheat	+
Mustard	Root exudate	Buckwheat	+
Couch grass	Grown as companion	Wheat	-
Common milkweed	Leaf extract	Grain sorghum	-
Chenopodium album	Root extract	Maize	-
Giant foxtail	Decaying roots	Maize	-
Wheat	Grown as companion	*Chenopodium album*	-
Oats	Grown as companion	*Chenopodium album*	-
Buckwheat	Grown as companion	*Chenopodium album*	-
Oats	Grown as companion	*Erysimum cheiranthoides*	-
Wheat	Grown as companion	*Sinapis arvensis*	-
Rye	Grown as companion	*Sinapis arvensis*	-
Barley	Grown as companion	*Sinapis arvensis*	-
Panicum miliaceum	Grown as companion	*Sinapis arvensis*	+

+ = stimulation of some parameter of growth
- = inhibition of some parameter of growth

The fact that some workers have tested for allelopathic agents in water soluble root exudates, whilst others have extracted various parts of the plant with hot or cold water, or organic solvents, has made it difficult to compare the results obtained, since different methods with different plants (parts) will vary in the efficiency with which the agents are solubilized. Of these methods, an aqueous solution of root exudates would appear to be representative of the *in vivo* situation. The different parts of a plant that contain or produce allelopathic agents are discussed later.

Much work has been performed on the allelopathic effects of weeds on crop plants. Minar (1974) reported that the production of fresh and dry matter of wheat tops was reduced when the weed couch grass (*Agropyron repens* L) was grown as a companion. Addition of fertilizer could not overcome the effect of couch grass completely even when other possible competitive mechanisms were effectively eliminated. Subsequent work indicated that couch grass chiefly reduced phosphate uptake by wheat, even when available phosphate was present in adequate amounts.

Common milkweed (*Asclepias syriaca* L) is a major weed in the United States and Canada, and was found to reduce the yield of grain sorghum significantly in field tests in Nebraska (Rasmussen and Einhellig, 1975). These workers demonstrated that aqueous extracts of milkweed leaves significantly inhibited the growth of grain sorghum seedlings, and reduced concentrations of the extracts resulted in proportional increases in yield. Kossanel et al (1977) reported that water solutions in which *Chenopodium album* L previously grew, and water extracts of ground roots of that species inhibited the growth of maize.

The growth and yield reductions of corn by infestations of giant foxtail (*Setaria faberii* Herm.) have been well documented, and were always ascribed to competition. However, Schreiber and Williams (1967) demonstrated that decaying roots of giant foxtail inhibited the growth of maize roots markedly. They also found that decaying roots of yellow foxtail (*Setaria glauca* (L) Beaur) and crabgrass (*Digitaria sanguinalis* (L) Scop) inhibited the growth of maize roots.

Crop plants have also been reported to have allelopathic effects on weeds. Neustruyeva and Dobretsova (1972) found that wheat, oats and buckwheat suppressed the growth, accumulation of above-ground plant mass and leaf area of *Chenopodium album*. Markova (1972) found that oats suppressed the growth of *Erysimum cheiranthoides* L owing at least in part to an allelopathic mechanism. Prutenskaya (1974) reported that wheat, rye and barley strongly inhibited the weedy *Sinapis arvensis* whereas *Panicum miliaceum* stimulated the growth of *S. arvensis*.

Some plants have been reported to inhibit the metabolism of bacteria in the soil. *Aristida adscensionis* Linn is a common grass species in abandoned lands at Rajkot, India. Because of previous evidence which indicated that *A. oligantha* is inhibitory to nodulation of legumes and haemoglobin formation in the nodules, Murthy and co-workers decided to determine if *A. adscensionis* was inhibitory to *Azotobacter, Rhizobium* and nodulation of *Indigofera cordifolia*, a

common associate of *A. adscensionis* (Murthy and Ravindra, 1974, 1975; Murthy and Nagodra, 1977). It was found that shoot and root extracts and leachates of *Aristida* residues were inhibitory to *Rhizobium* isolated from nodules of *I. cordifolia* and to *Azotobacter*, a free-living nitrogen-fixing bacteria. They also found that the numbers of nodules of *Indigofera* in association with *Aristida* in the field were lower than on the *I. cordifolia* growing where *Aristida* was absent. These workers suggested that inhibition of nitrogen-fixation might prevent species with higher nitrogen requirements from invading these fields and thus allow *Aristida* to remain dominant for a long time.

2.2 Allelopathic Effects of Microorganisms

The chemical activities of microorganisms are very important in determining both the distribution and growth of plants. Turner (1971) reviewed the many types of compounds produced by fungi and of these many are known to be phytotoxins which can inhibit the growth of other microorganisms and of higher plants. Many of them are important antibiotics which are used in the treatment of human ailments.

The inhibition of nitrogen-fixation by soil bacteria has recently attracted much attention. Chan et al (1970) reported how *Azotobacter chroococcum*, a common free-living nitrogen-fixer in the soil, was inhibited by *Pseudomonas* sp, and a rhizosphere isolate. Hussain and Mallik (1972) tested 28 species of fungi and 18 species of bacteria isolated from the rhizosphere of *Trifolium alexandrinum* against *Rhizobium trifolii* Dang., the root nodule bacterium in *T. alexandrinum*. Two species of fungi and two of bacteria were antagonistic and two species of bacteria were stimulating. Mallik and Hussain (1972) tested 41 species of fungi, 62 species of bacteria and 24 species of actinomyceters from the rhizosphere of lucerne (*Melilotus alba* Desr.) against two isolates of *Rhizobium meliloti* from lucerne nodules. Five per cent of the fungi, 14% of the bacteria, and 21% of the actinomycetes exerted antagonistic effects, whereas 7% of the fungi and no bacteria or actinomycetes were stimulatory.

2.3 Allelopathic Effects of Algae

The fluctuations in abundance and kinds of phytoplankton in bodies of water have provided areas for the study of allelopathy. Akehurst (1931) suggested that allelopathic agents might be produced by blooms of algae and that these cause algal succession by inhibiting some species and not others. Berglund (1969) described how certain green algae grew better when cultivated in sea water taken from the *Fucus-Ascophyllum* zone off the west coast of Sweden, than when cultivated in surface water collected 100 m from shore. Growth was poor also in sea water taken from a depth of 30 m, even after enrichment with nutrients. Growth was stimulated in free surface water and in deep water if certain living algae (*Ulva, Chorda, Ceramium, Ascophyllum, Chondrus, Fucus*) were previously placed in the water for 24 hours.

Many investigators have collected and identified the allelopathic compounds excreted by various algae. Fenical (1975) described the many halogenated compounds produced by various red algae; and

these included halogenated phenols, monoterpenes, sesquiterpenes and diterpenes. Murphy et al (1976) reported that excretion of hydroxamate chelators by certain blue-green algae ties up iron and makes it unavailable to other algae, inhibiting their growth.

Gupta and Houdeshell (1976) have now included a category of allelopathic effects of algae on other algae and allelochemic effects of algae on zooplankton in a differential-difference equations model of a dynamic ecosystem. Rice (1979) has predicted that in future, all meaningful, functional ecological models will include a category for allelopathy and other allelochemic effects.

In any study of algal dominance in a given ecosystem, attempts should always be made to distinguish between seasonal cycles and allelopathic effects, in that the former may be mistaken for the latter. Early studies may not have made this distinction.

2.4 Allelopathic Effects of Woody Plants, In Particular Trees

The black walnut (*Juglans nigra*) provides one of the best known examples of a tree that has an adverse effect on other plant species growing under its leaf canopy. Early work by Stickney and Hoy (1881) described how the vegetation under black walnut was very sparse compared with that under shade trees, and how no crop would grow under it or near it. Cook (1921) reported the characteristic wilting of potato (*Solanum tuberosum*) and tomato (*Lycopersicum esculentum*) plants grown near black walnut, and its injurious effects on apple trees. Perry (1932) related that black walnut could kill both white pine (*Pinus strobus* L.) and black locust (*Robina pseudoacacia* L.) growing near. The compound responsible for this allelopathic effect is juglone, a hydroxyquinone formed in the soil by hydrolysis of 1,4,5-Trihydroxynaphthalene-4-glucoside released by the leaves and washed off by rain and dew. Juglone remains in the soil for long periods (three years or more) and is still inhibitory (Gabriel, 1975). Some plant species are not inhibited by juglone, Kentucy blue-grass (*Poa pratensis*) has evolved a defensive mechanism (Bell, 1981).

Baranetsky (1973) found that water extracts of fallen leaves of European ash (*Fraximus excelsoir* L.) were inhibitory to several test plants, and were found to contain large quantities of a cyanogenic glucoside. Water extracts of *Tilia cordata* Mill. contained potent inhibitors also, and extracts of both species contain indole and gibberellin-like growth stimulators.

Thomas (1974) used aqueous extracts of blue spruce (*Picea pungens* Engelm) to moisten filter paper on which seeds of grasses and cereals were allowed to germinate. The extracts caused malformed roots, blackened root tips, and a lack of root-hair development.

Kuhn et al (1943) reported that the mountain ash (*Sorbus aucuparia*) produces parasorbic acid, an unsaturated lactone, which inhibits the germination of *Lepidium* seeds in a dilution of 1 in 1000 and allows only 10 to 80% germination at 1 in 10,000.

The rocky mountain juniper (*Juniperus scopulorum* Sarg) produces both water soluble and volatile inhibitors which reduce germination of several herbaceous species, including grasses, which grow at the same altitude as the tree (Peterson, 1972).

There have been other reports of allelopathic effects of tree species on other tree species. Nursery experiments in Michigan showed that the presence of seedlings of sugar maple (*Acer saccharum* Marsh) inhibited the growth of seedlings of yellow birch despite the apparent absence of competition (Tubbs, 1973). Root elongation of birch was found to be inhibited by exudates of actively growing root tips of sugar maple. The toxin lost its inhibitory activity after a few days storage. When seedlings of the two species were grown together in an aerated nutrient solution, the number of actively growing root tips of birch formed each day was inversely correlated with the activity of the inhibitor as indicated by its retardation of elongation of roots of yellow birch in a bioassay.

2.5 Allelopathic Effects on Non-Woody and Woody Plants on Trees

Brown (1967) observed that on a similar site, jack pine (*Pinus banksiana*) stands ranging from a few stems to 1000 or more per acre may be found within a few yards of each other. Ground cover plants showed similar extremes in density. Measurements of soil texture, available minerals, depth of water table, water-holding capacity, soil acidity, root competition, slope exposure, microclimate, and seed dispersal did not reveal differences that explained the variation in jack pine stand density. Since there were no differences in logging or fire history, Brown attempted to identify naturally occurring, biologically active materials which affect jack pine seed germination and growth. In a comprehensive study, water extracts of 56 species of plants commonly associated with jack pine were used as the moistening medium for germination of seeds in the laboratory. Nine of the extracts were found to inhibit the germination of jack pine seeds. Two species of *Prunus* completely inhibited germination, and two species of *Solidago* and *Salix pellita* almost completely inhibited it (see Table 2). The pH of the extract was not a factor since it varied greatly in both the non-inhibitory and inhibitory extracts. Brown found that all species that consistently inhibited germination of jack pine seeds in the laboratory tests were similarly inhibitory in the field. Brown's experiment did not permit any conclusion to be drawn concerning the role of allelopathy in the subsequent growth of the seedlings. It may be that once germination has taken place, the young seedling is more or less sensitive to allelopathic agents.

The presence of sheep laurel (*Kalmia angustifolia* L) on upland sites in eastern Canada appears to be associated with abnormally poor tree growth (Peterson, 1965). Bioassays indicated that dry leaves of *Kalmia angustifolia* contain a water and ethanol soluble substance that hinders primary root development of black spruce *Picea mariana* Mill) by destruction of epidermal and cortical cells.

TABLE 2

GERMINATION OF JACK PINE SEEDS
IN THE PRESENCE OF INHIBITORY PLANT EXTRACTS

Species	Plant Part Extracted	pH of Extract	Percent Germination After 17 Days
Boletus edulis	fruiting bodies	-	37
Cladonia cristatella	Plants	5.1	24
Sphagnum capillaceum	Plants	4.6	22
Salix pellita	Leaves	6.2	9
Prunus pumila	Leaves	-	0
Prunus serotina	Leaves	6.2	0
Gaultheria procumbens	Leaves	6.3	21
Solidago juncea	Flowers	-	11
Solidago juncea	Leaves	5.0	9
Solidago uliginosa	Leaves	-	2
Control	-	-	82

From Brown (1967)

Grass residues have also been reported to reduce germination of tree seeds. Rietveld (1975) found that water extracts of green foliage of Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) reduced germination of ponderosa pine (*Pinus ponderosa*) seeds, and retarded speed of elongation and mean radicle length. Rietveld (1975) did point out that coincidence of toxic levels of the inhibitor with initial growth processes appears to be necessary.

Horsley (1977 b) observed that in a comparison of paired field plots, the presence of hay-scented fern (*Dennstaedtia punctilobula* Michx), New York fern (*Thelypteris noveboracensis* L), short husk grass (*Brachyelytrum erectum* Schreb), and club moss (*Lycopodium obscurum* L) was correlated with reduced numbers of black cherry (*Prunus serotina* Ehrh) seedlings; numbers of red maple (*Acer rubrum* L) seedlings were fewer where associated with the ferns and grass but not with club moss; numbers of sugar maple (*Acer saccharum* Marsh) seedlings were fewer with the ferns but not grass or club moss. In a greenhouse study, foliage extracts of all four ground covers inhibited growth of black cherry seedlings that had exhausted cotyledonary reserves. In an earlier study (Horsley, 1977 a), a foliage extract of bracken fern (*Pteridium aquilinum* L), wild oat grass (*Danthonia compressa* Aust.), goldenrod (*Solidago rugosa* Ait), and flat-topped aster (*Aster umbellatus* Mill.) inhibited both germination of black cherry seeds and shoot growth and dry weight accumulation of seedlings that had exhausted cotyledonary reserves. Bracken fern (*Pteridium aquilinum* L) had earlier been investigated by Gliessman (1976). He described bracken as being an extremely opportunistic plant, well known for its plasticity in response to the environment and maintaining dominance through variations of the allelopathic process. In southern California, phytotoxin release is timed for the initiation of the wet season (and thus the initiation of germination of associated plants), with toxins coming primarily from the dead, standing fronds. In the Pacific Northwest, toxin release is timed for the breaking of dormancy in spring, with toxins coming primarily from bracken litter, roots and rhizomes. In Costa Rica, toxins produced in the green fronds are released all year long. In a series of field, greenhouse and laboratory studies, Fisher et al (1978) reported that both goldenrod (*Solidago canadensis*) and aster (*Aster novae-angliae*) produced water soluble compounds that inhibited germination, nutrient uptake and growth of sugar maple (*Acer saccharum* Marsh.).

3.0 PLANT PARTS THAT CONTAIN ALLELOPATHIC AGENTS

Although many workers have used combinations of plant parts (eg, the whole plant) as a source of allelopathic agents, some investigators have separated plants into their various parts.

Leaves seem to be the most common source of inhibitors, and most investigators have tested them, either alone or in combination with other plant parts. They have been shown by many workers to contain toxins (for a review see Rice, 1974). Stems have not been tested separately in many experiments; however, some have been shown to contain inhibitors, and in a few instances they are the chief source of toxicity (Rice, 1974). Although roots have generally less potent inhibitors than leaves, this is sometimes

reversed (Rice, 1974). Toxins have also been found in fruits, seeds and flowers or inflorescences. The toxins in seeds afford protection against microbial activity that leads to decomposition and to seed decay. Rice (1979) comments that this is one of the most important and universal roles of allelopathy in natural ecosystems; but little research has been done in this area (Rice, 1974).

4.0 RELEASE OF ALLELOPATHIC AGENTS FROM PLANTS

Since Elmer (1932) demonstrated that volatile substances emanating from apples inhibited the growth of potato sprouts, many volatile inhibitors have been identified. The genus *Eucalyptus* has been shown to produce several volatile terpenes, some of which are toxic to seed germination and seedling growth of numerous plant species (del Moral and Muller, 1970). Although leaves of *E. camaldulensis* were found to emit large amounts of terpenes toxic to plant growth, leaf litter, bark, and roots did not produce significant amounts (del Moral and Muller, 1970). Muller (1970) and Whittaker (1970) have proposed that volatilization would predominate in an arid climate whilst leaching (see below) would predominate in a humid climate. Data obtained by del Moral and Cates (1971) provide support for such a hypothesis. Biologists have been aware of the leaching phenomenon since early in the eighteenth century, and many kinds of inorganic ions, elements and compounds (organic and inorganic) have been identified in the leachate of plant foliage (Tukey, 1966, 1969, 1971). Lee and Monsi (1963) found a statement in ancient Japanese documents approximately 300 years old which described how rainwater or dew from the leaves of *Pinus densiflora* was harmful to crops underneath. The fact that extracts of various plant parts contain phytotoxins does not necessarily mean that they will leach or exude from the plant. However, water-soluble toxins present in a plant, will generally leach out after death. The list of plants shown to contain growth inhibitors in leachates from living and/or dead leaves is enormous (for a review see Rice, 1974).

Lyon and Wilson (1921) first demonstrated that roots of several crop plants exuded large amounts of organic compounds even under sterile conditions. Schreiner and Reed (1907) and Schreiner and Sullivan (1909) demonstrated that wheat, oats, corn and cowpeas produced inhibitory root exudates. More crop plants have been added to this list: guayule (Bonner and Galston, 1944), a non-nodulating soybean (Elkan, 1961), and cucumbers and tomatoes (Gaidamak, 1971). Noncrop plants have also been shown to produce toxic root exudates - *Sorghum halepense* (Abdul-Wahab and Rice, 1967), *Euphorbia supina* (Brown, 1968; Rice, 1968) and *Helianthus annuus* (Rice, 1968).

It is difficult to show that inhibitors already present in plants are released by decay, since there is a possibility that certain microorganisms are changing nontoxic compounds to toxic ones (as is the case of amygdalin in peach residues) Patrick, (1955). However, Rice (1974) quotes many examples of plants in which inhibitors are released from their residues during decay eg wheat, oats, barley, rye, corn, sorghum and apple.

5.0 ALLELOPATHIC AGENTS (INHIBITORS) - CHEMICAL NATURE AND MECHANISM OF ACTION

Most allelopathic agents are compounds termed secondary metabolites (Fraenkel, 1959; Whittaker and Feeny, 1971) since they have no recognized role in the maintenance of fundamental life processes in the organisms that synthesize them (Bell, 1981). There are many thousands of secondary metabolites (see Swain, 1977), but only some have been identified as toxins involved in allelopathy. Rice (1974) has divided those secondary metabolites with allelopathic properties into 14 groups (see Figure 1). The list of allelopathic agents includes simple phenolic acids, coumarins, terpenoids, flavonoids, alkaloids, cyanogenic glycosides, and glucosinolates. The most outstanding characterstic of this list is its diversity. The probable biosynthetic pathways leading to the production of these compounds are based on the work of Neish (1964), Brown (1964) and Robinson (1963). It is interesting that most of these compounds arise either through the acetate or the shikimic acid pathways.

Shikimic acid, a hydroaromatic acid, is a key intermediate in the pathway in which aromatic amino acids are synthesized from purely alipathic precursors. The mechanism of aromatization employed in this pathway, is of great significance, since it extends well beyond the formation of the aromatic amino acids. Enormous quantities of lignin, a polymerized aromatic substance making up a substantial portion of the woody portions of plant tissues, are synthesized via shikimic acid, as are many other aromatic biomolecules such as ubiquinone and plastoquinone, which are involved in electron transfer processes in mitochondria and chloroplasts respectively. Acetate is a key intermediate in the respiratory pathway.

It is still not known whether these allelopathic compounds are end products of metabolism or are actually synthesized by the plant for specific functions. It has not yet been proven that these compounds are specifically synthesized as the result of an external stimulus, although related secondary metabolites would seem to be continually synthesized and degraded in healthy plant cells and may be under genetic control (Barz and Hösel, 1975; Swain, 1977).

The mechanisms of action of allelopathic agents have received more attention of late (Rice, 1979). In such studies it has proved difficult to distinguish between secondary effects and primary causes, however a variety of effects have been documented.

Inhibition of cell division has been widely reported. Jankay and Muller (1976) found that umbelliferone caused a decrease in the rate of cell elongation in cucumber roots, and at the same time an increase in radial expansion. Exposure of cucumber roots to volatile terpenes from *Salvia leucophylla* leaves caused accumulation of globules (apparently lipid) in the cytoplasm of root tip cells, a drastic reduction in the number of a variety of organelles including mitochondria, and disruption of membranes surrounding nuclei, mitochondria and dictyosomes (Lorber and Muller, 1976).

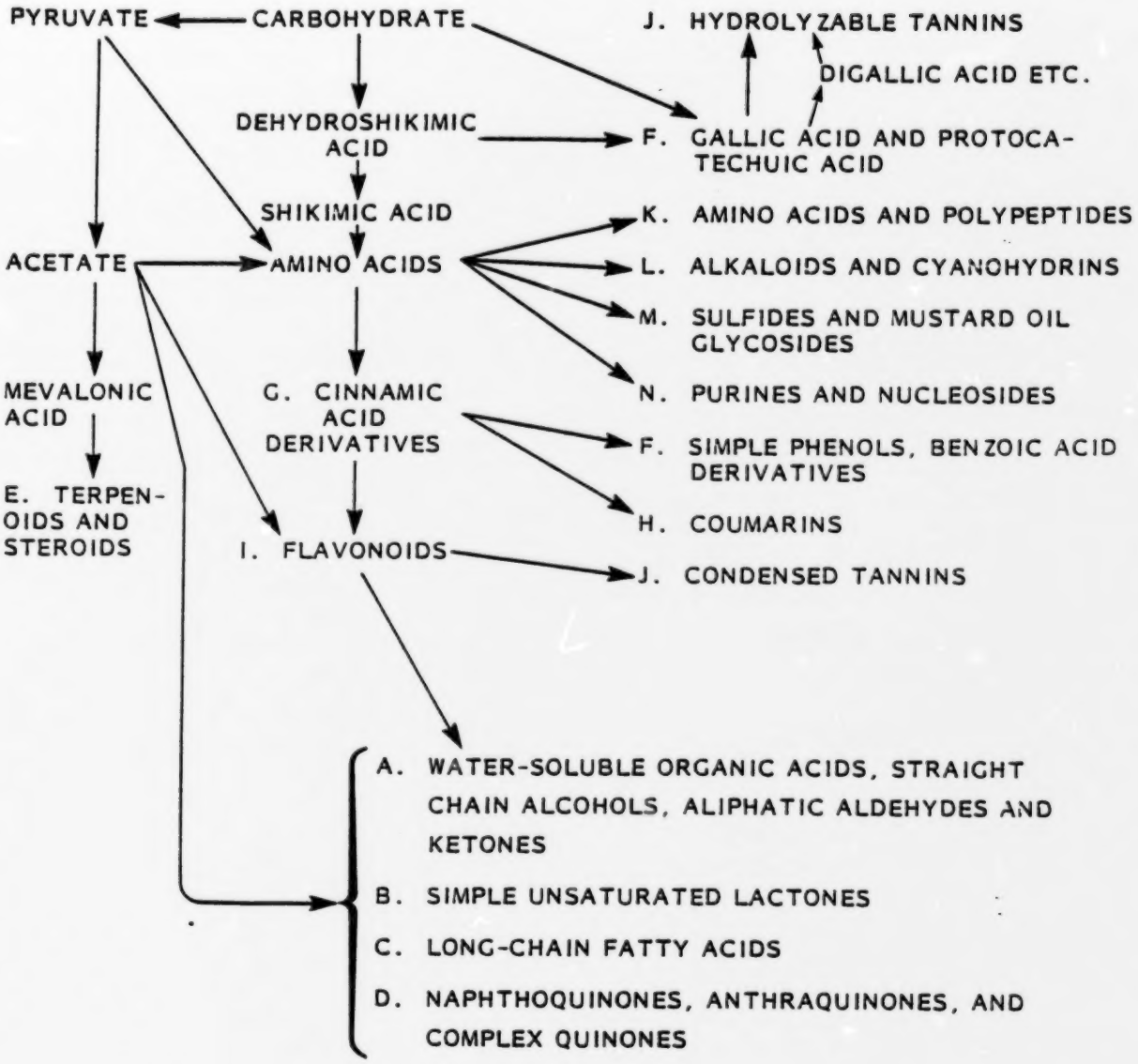

FIGURE 1

CLASSES OF ALLELOPATHIC CHEMICALS AND THEIR PROBABLE PATHWAYS OF SYNTHESIS

(FROM RICE, 1974)

Several allelopathic compounds have been found which affect hormone-induced growth (Rice, 1974). The toxin produced by *Fusarium tricinctum* inhibited auxin-promoted elongation in soybean (*Glycine max*) (Stahl et al, 1973). Corcoran demonstrated that some tannins inhibited gibberellin-induced growth in dwarf-pea seedlings (Corcoran et al, 1972; Green and Corcoran, 1975). She also found that coumarin, cinnamic acid, and several phenolic compounds were less effective in inhibiting such growth. Inhibition could be completely reversed in all cases by increasing the amount of gibberellin applied.

The first indication of damage to cells caused by pathogen produced phytotoxins is an alternation in water and ion permeability of the cytoplasmic membrane (Owens, 1969). Keck and Hodges (1973) reported that the toxin (victorin) produced by *Helminthosporium victoriae* dramatically increased the permeability of both the plasma membrane and tonoplast of root cells in a susceptible cultivar of *Avena sativa*, but not in a resistant cultivar. Aescin, a triterpeneglycoside, induced leakage of ribonucleotides, nucleosides and pentoses from hyphae of *Ophiobolus graminis* and *Neurospora crassa* (Olsen, 1975). Loss of viability seemed to be correlated with the loss of oligonucleotides from the cells. Salicylic acid [found in the oak (*Quercus falcata*), among others (Bell, 1981)] was found to reduce the potassium content of commercial baker's yeast, by allowing it to leak out (Rice, 1974).

Allelopathic compounds have pronounced effects on ion uptake by plant roots. Glass has conducted a thorough investigation into the effects of the most commonly cited class of compounds the phenolic acids on ion uptake by barley (*Hordeum vulgare*) roots (Glass, 1973; Glass and Dunlop, 1974; Glass 1975). All phenolic acids tested inhibited ^{32}P-labelled phosphate uptake, and the degree on inhibition correlated with the lipid solubility of the compounds. The membrane potentials of barley root cells were rapidly depolarized by several benzoic and cinnamic acid derivatives, and there was a strong positive correlation between the depolarization values for the benzoic acids and their lipid solubilities. Glass concluded that his studies supported the hypothesis that the inhibition of ion uptake is caused by a generalized increase in membrane permeability of inorganic ions.

Kolesnichenko and Aleikina (1976) reported that absorption of minerals from soil is lower in oak roots (*Quercus robur*) growing close to the roots of ash (*Fraxinus excelsior*) than in oak roots growing near other oak roots. In the laboratory the uptake of mineral by oak roots was inhibited by chemical compounds isolated from ash roots.

The inhibition (or stimulation) of ion uptake by allelopathic compounds appears to be the result of a direct effect on the membrane-bound plasma membrane ATPase involved in ion transport (Balke, 1977; Balke and Hodges, 1977). Balke (1977) tested various phenolic compounds for their effects on K^+ absorption by excised oat (*Avena sativa*) roots and on ATPase activity of plasma membrane vesicles isolated from oat roots. Flavonoids were generally more inhibitory than phenolic acids (of the latter the most inhibitory tested was juglone). The synthetic diphenolic compound diethylstilbestrol (DES) markedly inhibited K^+ and Cl^- absorption

by excised oat roots and inhibited the plasma membrane ATPase also (Balke, 1977; Balke and Hodges, 1977). The plasma membrane of some plant species and tissues has a protein that functions in the transport of alpha-galactosides such as melibiose and raffinose. This has been inferred from the demonstration that the plasma membrane of susceptible sugarcane plants contains a protein that binds the toxin, helminthosporoside, produced by the fungus *Helminthosporium sacchari* (Strobel, 1975). The toxin is a complex sugar similar in structure to the alpha-galactosides. The toxin-binding protein has been purified and shown to bind the sugars more strongly than the toxin. Although it is not known how binding the toxin to the sugar transport protein leads to disease symptoms, it seems that toxin binding to the membrance-associated binding protein may alter other transport systems leading to a disruption of membrane function and cell death (Leonard and Hodges, 1980).

Photosynthesis is also inhibited by allelopathic compounds (Rice, 1974). Roshchina (1973) investigated the effects of water infusions of twenty woody plant species on photochemical reactions of photosynthesis in isolated chloroplasts. Infusions of *Juglans regia* and *Betula verrucosa* leaves contained polyphenols which inhibited photochemical reactions (the former also contained juglone). Boiled aqueous leaf extracts of *Celtis laevigata*, a known allelopathic species, inhibited CO_2 uptake by three grass species when added to the nutrient solution in which the grasses were growing (Lodhi and Nickell, 1973). Arntzen et al (1974) reported that kaempferol, a known allelopathic flavonoid, inhibited coupled electron transfer and both cyclic and noncyclic photophosphorylation in isolated pea (*Psium sativum*) chloroplasts. There was no effect on basal or uncoupled electron flow or light-induced proton accumulation by isolated thylakoids over a concentration range which markedly inhibited ATP synthesis. These workers suggested that kaempferol acts as an energy transfer inhibitor. In an earlier report (Arntzen et al, 1973) it was found that the toxin produced by *Helminthosporium maydis* has a direct effect on stomatal functioning in leaves of susceptible corn (*Zea mays*). The toxin inhibited light-induced K^+ uptake by guard cells, and thus the stomates did not open.

Weaver and Klarich (1977) found that vapours from *Artemisia tridentata* reduced respiration rates of germinating seeds of wheat and cucumber, and of newly emerged leaves of wheat and barley. The vapours stimulated respiration in mature leaves of wheat and oats, two species of *Juniperus*, four species of *Pinus*, douglas fir and two species of *Picea*.

The flavonoid kaempferol has been found to act on both the phosphorylation mechanism and on electron transfer in isolated plant mitochondria (Koeppe and Miller, 1974; Ravanel et al, 1982). Koeppe (1972) had earlier reported that juglone uncoupled ATP production in corn mitochondria, and that this finding correlated well with the inhibition of respiration that results when tissues or organisms are treated with juglone. Salicylaldehyde, cinnamaldehyde, cinnamic acid, o-courmaric acid and scopoletin were all reported to be uncouplers by Van Sumere et al (1971). Rice (1974) states that since many identified allelopathic agents have adverse effects on respiratory activity by isolated respiratory

enzymes, isolated mitochondria, single cell organisms, and organs of plants, this suggests that respiratory effects may represent an important mechanism of action of at least some inhibitors.

The rate of protein biosynthesis in roots of oak (*Quercus robur*) growing close to the roots of ash (*Fraxinus excelsior*) is lower than in roots of oak growing with other oak trees (Kolesnichenko and Aleikina, 1976). In laboratory studies, protein synthesis in oak roots was inhibited by chemicals isolated from ash roots. Specific enzymes are also affected by allelopathic agents. Jankay and Muller (1976) found that umbelliferone caused cucumber roots to swell, and that increased peroxidase activity appeared coincident with this swelling response. It was suggested that higher peroxidase activity may be involved in the mediation of radial expansion.

Bogdan and Grodzinsky have published several papers on the non-specific effect of allelopathic agents in causing the corking and clogging of xylem elements (Bogdan, 1971, 1977; Bogdan and Grodzinsky, 1974). Histochemical tests indicated that the brown substance which impregnated the walls and filled the cavities of the vessels of these plants treated with aqueous extracts of known allelopathic species, was a complex of pectin, lignin, suberin, melanin and other unknown substances. The allelopathic agents caused an increase in the amount of the reduced form of ascorbic acid in the xylem, and thus somehow promoted formation of the brown substance. A few papers have been published on the effects of allelopathic agents on stem conductance of water and water relations of the plant in general. The wilting effects of allelopathic agents are well known (eg the wilting effect of Dutch elm disease) (Rice, 1979). Application of water-soluble glycopeptide toxins from cultures of *Ceratocystis ulmi* reduced the stem conductance of water in *Ulmus americana* seedlings by 79% (Van Alfen and Turner, 1975). The leaf potential was also reduced to the point at which the seedlings wilted, the stomates closed, and transpiration ceased.

6.0 ROLE OF ALLELOPATHY IN MANIPULATED ECOSYSTEMS

Although it is immediately apparent from the above discussions that allelopathic effects have been observed and characterized in a wide variety of ecosystems (and it may be that such effects occur in all ecosystems) man has not used such effects to his advantage to any great extent.

The role of allelopathy in manipulated ecosystems has been investigated most energetically in the agricultural area, with an examination of the allelopathic effects of crop plants on both weeds and other crop plants, and the effects of weeds on crop plants. Many such studies have concerned the allelopathic effects of decomposing crop residues. This probably resulted from the expanding use of stubble mulch farming since the "dust bowl" days of the 1930's to control erosion by wind and water and the resulting decreases in crop yields in many instances (for a review see Rice, 1974). Knowledge of the conditions under which certain crop residues cause allelopathic effects to subsequent crops will enable farmers to guard against such effects. It will be possible to

breed crop plants that inhibit the chief weeds in a given area by allelopathic action, and thus decrease the need for synthetic weed killers (ie, herbicides).

As in agriculture, the incentives which have promped investigations into the roles of allelopathy in forestry have been economic in nature. The widespread occurrence of woody species that are allelopathic to other species and sometimes to themselves has been alluded to in previous sections of this review. Reforestation programs are already benefiting from a knowledge of allelopathic interactions of various plants, and again the use of herbicides in the future to control competing weed species may be reduced as a direct result.

7.0 ROLE OF ALLELOPATHY IN SUCCESSION

As mentioned in an earlier section, the role of algal allelopathy in succession is fundamental. Before considering this role and the role of allelopathy in a terrestrial environment, it might be propitious to describe briefly the process of ecological succession.

In an ecosystem such as a pond or a section of right-of-way, the complex assemblage (community) of living organisms is subject to change in physical structure and species composition over time (ecological succession) (Kimmins, 1975). The process of ecological succession continues until a biotic community is establisheed that either is unable to create sufficient environmental change to permit its replacement by a succeeding community, or that represents the most competitive community existing in the region. This final community, which is relatively stable and unchanging, is referred to as the climax community.

Various terms, such as blooms and pulses, have been used to refer to the rapid increases in numbers of phytoplankton above the numbers that previously existed in a given area (Rice, 1974). The blooms are sometimes due to either an increase in the number of one species or an increase in the numbers of several species. Such blooms often disappear as rapidly as they appear.

The abundance of each phytoplankton species, the size of the total population, and the succession of dominant species during the growing season may all be influenced by allelopathic interactions between the various species. Many species of algae have been identified which produce compounds which inhibit or stimulate the growth of other algal species.

In terrestrial environments there are several well-documented examples of the effects of allelopathy in succession. In the tall grass prairie region of Oklahoma and Kansas, there are four main successional stages after fields, low in fertility, are abandoned from cultivation (Rice, 1974):

i) pioneer weed stage,
ii) annual grass stage,
iii) perennial bunch grass, and
iv) climax prairie

The first stage lasts only 1 to 2 years whilst the second stage lasts from 9 to 13 years and is dominated by triple own grass (*Aristida oligantha* Michx). The perennial bunch grass state is dominated by little bluestem (*Schizachyrium scoparium*) and is still present 30 years after abandonment. The pioneer weed stage disappears rapidly because the species eliminate themselves through strong allelopathic interactions, and *A. oligantha* invades because it is not inhibited by the phytotoxins produced and is able to grow well and reproduce in soil that is still too low in nitrogen and phosphorus to support species that come later in succession (Rice, 1974). Leuck and Rice (1976) reported that the allelopathic activity of rhizosphere bacteria of *A. oligantha* against free-living nitrogen-fixing bacteria found in the soil complements a direct effect of *A. oligantha* on such bacteria (by the production of phytotoxins) and this delays nitrogen accumulation in the soil and prolongs the annual grass stage.

Although the process of succession described above culminates in a climax prairie stage, there are examples of the grass stage being followed by a shrub stage, and then ultimately a tree stage. A similar pattern of development occurs if a landslide exposes a surface of rock in the mountains, the surface may be successively occupied by a sparse cover of lichens; a spreading moss mat; grasses, which enter and become a meadow; a shrub thicket, which overtops and suppresses the grasses; a first forest stage of smaller trees, which seed into the shrub thicket, grow through it, and replace it; and a final stage of large trees, which take dominance from the first trees and may form a larger and potentially permanent forest community (Whittaker, 1970). The role of allelopathy in such a climax forest community is poorly documented (Rice, 1974, 1979).

Although there are many examples of trees inhibiting the growth of the understory (and vice versa), there has been no attempt to integrate such findings into an overall description of the complex interrelationships that exist in a climax forest ecosystem, let alone in an ecosystem which has not reached such a steady-state condition. In fairness, it would be extremely difficult to describe the role of allelopathy (and distinguish it from competition effects) in such a complex ecosystem.

8.0 POSSIBLE ROLE OF ALLELOPATHY IN VEGETATION CONTROL ON RIGHTS-OF-WAY

At present, Ontario Hydro uses a combination of mechanical clearing and herbicides to control the vegetation under transmission lines. Both techniques retard ecological succession. Manual control of vegetation may have many effects similar to those of herbicidal control, but the absence of toxicological effects is highly desirable. Reforestation is an area where serious consideration has been given to utilizing plants rather than herbicides to achieve more efficient production of biomass. In choosing the crop species, it may be better in economic terms to pick one that is able to compete effectively with or tolerate the competition of the weed species, rather than control such weeds with herbicides (and incur an additional expense at the same time). In what would be the reverse situation, little consideration has been given to using non-woody species (eg weeds) to control incompatible woody species and other vegetation on rights-of-way.

Such an approach would be feasible since a number of such species have been identified, although few woody species were reported to be susceptible simply because few were screened for technical reasons. For example, sheep laurel (*Kalmia angustifolia* L.) has been shown to inhibit the growth of black spruce (*Picea mariana*) (Peterson, 1965). While both hay-scented fern (*Dennstaedtia punctilobula*) and New York fern (*Thelypteris noveboracensis*) inhibit the growth of black cherry (*Prunus serotina*) and red maple (*Acer rubrum*) (Horsley, 1977 b). The perennials *Solidago juncea* and *S. uliginosa* inhibit the growth of jack pine (*Pinus banksiana*) (Brown, 1967). Given the number of allelopathic agents which have been identified and the wide variation in the response of plants exposed to such agents, it is probable that specific non-woody plant species may only adversely affect the growth of a small number of tree species. The effects of allelopathic agents on seed germination may also be important, since after mechanical clearing of a right-of-way, some of the vast number of tree seeds buried in the soil will germinate, and ultimately cause as much a problem as will invasion from the edge of the right-of-way.

The choice of allelopathic plant to introduce onto a right-of-way after clearing to hinder the invasion of problem species would be difficult. Firstly, it should adversely affect the germination and growth of the problem species in question - however should there be more than one problem species, then a combination of allelopathic plants may be required to give a broad spectrum of effects. Once an allelopathic plant has been introduced, it may not survive from year to year, as the environmental conditions (soil type etc) may not be conducive to prolonged growth. Should the plant survive, consideration should be given to the rate of breakdown (under the given conditions) of the allelopathic agent, since some agents (eg juglone) only break down slowly, and a build-up of agent may cause problems in the future. In many ways this last concern is similar to the problem encountered with some herbicides - that of residual activity remaining in the soil. If the allelopathic plant grows successfully, it may spread off the right-of-way and cause problems in neighbouring areas ie adjacent fields (such an example would be couch grass (*Agropyron repens* L) which can cause problems in agricultural areas because its rhizome form is difficult to remove). In non-agricultural areas, such as Northern Ontario, this concern may not be a problem however. The choice of allelopathic plant should not be limited to existing stock, since it may be possible to use both conventional breeding techniques and recombinant DNA techniques to produce a more effective plant.

At present Ontario Hydro does plant various cover crop species on clear cut rights-of-way to prevent soil erosion and to resist the invasion of incompatible woody species (in part through allelopathic effects). Of the five grass and six legume species used as cover crops, timothy (*Phelum pratense* L.) has been reported to be allelopathic to crop plants (Patrick and Koch, 1958).

9.0 CONCLUSIONS

The existence of allelopathy has been well documented in recent years, particularly in relation to its significance in natural and agroecosystems. However, research efforts have been hampered by several major difficulties, including a lack of reliable techniques to separate allelopathic influences from other aspects of interference such as competition. The overall approach to allelopathy methodology has been varied, and techniques need to be developed to effectively isolate the suspected compounds, identify them, and to demonstrate that the isolated substance actually caused the observed effects. The suspected chemical could then be synthesized and compared with the natural product in terms of activity. Because of poor methodology, many allelopathic agents that are effective at low concentrations remain to be discovered.

New instrumentation that has been developed in recent years should greatly aid the isolation and identification of these natural products. Recent advances in high pressure liquid chromatography (HPLC) and gas liquid chromatography coupled to mass spectrometry (GLC-MS) should aid chemists in their search for unique allelopathic compounds.

The potential for exploiting allelopathy in agriculture and forestry is enormous. These areas are attractive because allelopathic agents produced by crop plants or trees in reforestation programs would only control weeds in the immediate vicinity of the 'donor', thus avoiding the undesirable effects of broadcast herbicides. With agronomic crops, the allelopathic mechanism could be selected for and perhaps incorporated into cultivars. Crop cultivars might be developed which would release kolines as natural herbicides, or alternatively a companion plant that is selectively allelopathic, but does not appreciably interfere with the crop plant, might be grown. The possibility that toxic compounds of plant origin accumulate in the soil, and have a variable life-span, might require that the utility of allelopathy be based on treatments of short duration. In the forestry industry, the prime consideration has been to exploit the deleterious effects of toxins produced by trees on the growth of weeds, whereas in vegetation control on rights-of-way the reverse situation would be exploited. Although allelopathy might have a role in the future in control of problem woody species on rights-of-way, it will be limited in that localized areas only may respond to such treatment methods.

Approved: Submitted:

D. Harrison
Manager
Chemical Research Dept

G.P. Arron
Biologist
Biological Research Section

GPA:aba

REFERENCES

Abdul - Wahab,A.S., Rice,E.L. (1967). Plant inhibition by Johnson grass and its possible significance in old-field succession. Bull. Torrey Bot. Club 94, 486-497.

Akehurst, S.C. (1931). Observations on pond life, with special reference to the possible causation of swarming of phytoplankton. J. Roy. Micros. Soc. (3) 51,237-265.

Arntzen, C.J., Falkenthal, S.V., Bobick, S. (1974). Inhibition of photophosphorylation by Kaempferol. Plant Physiol. 53, 304-306.

Arntzen, C.J., Haugh, M.F., Bobick, S. (1973). Induction of stomatal closure by *Helminthosporium maydis* pathotoxin. Plant Physiol. 52, 569-574.

Balke, N.E. (1977). Inhibition of ion absorption in *Avena sativa* L. roots by diethylstilbestrol and other phenolic compounds. Ph.D. Thesis Purdue University, In.

Balke, N.E., Hodges, T.K. (1977). Inhibition of ion absorption in oat roots: Comparison of diethylstilbestrol and oligomycin. Plant Sci . Lett 10, 319-325.

Baranetsky, G.G. (1973). On the chemical nature of the biologically active water-soluble substances in fallen ash and lime leaves. In Physiological-biochemical basis of plant interactions in phytocenoses. Vol 4, pp 85-88 (AM Grodzinski ed) Naukova Dumka, Kiev.

Barz, W., Hösel, W. (1975). Metabolism of flavonoids. In The Flavonoids. (J.B. Harbourne, T.J. Mabry, H. Mabry eds) pp 916-969, Chapman and Hall, London.

Bell, E.A. (1981). The physiological role(s) of secondary (natural) products. In The Biochemistry of Plants, A Comprehensive treatise. Vol 7 (E.E. Conn ed) Academic Press, New York.

Berglund, H. (1969). Stimulation of growth of two marine algae by organic substances excreted by *Enteromorpha linza* in unialgal and axenic cultures. Physiol. Plant. 22, 1064-1073.

Bogdan, G.P. (1971). Anatomical study of effects in the plant conducting system of allelopathic substances. Ukrajins'k Bot. Zhurn. 28, 703-707.

Bogdan, G.P. (1977). Mutual effect of couch grass and cultivated plants in phytocenoses. Interactions of plants and microorganisms in phytocenoses, pp 36-43 (A.M. Grodzinsky ed). Naukova Dumka, Kiev.

Bogdan, G.P., Grodzinsky, A.M. (1974). Role of sulf-hydryl groups in protective reactions in plants during allelopathic damage. Ukrajins'k Bot. Zhurn 30, 771-778.

Bonner, J., Galston, A.W. (1944). Toxic substances from the culture media of guayule which may inhibit growth. Bot. Gaz. 106, 185-198.

Brown, S.A. (1964). Lignin and tannin biosynthesis. In Biochemistry of Phenolic Compounds (J.B. Harbourne ed) pp 361-398. Academic Press, New York.

Brown, R.T. (1967). Influence of naturally occurring compounds on germination and growth of jack pine. Ecology 48, 542-546.

Brown, D.D. (1968). The possible ecological significance of inhibition by *Euphorbia supina*. M.Sc. Thesis University of Oklahoma, Norman.

Bykov, B.A. (1970). Vvedenie v fitocenologiju. "Nauka" Alma-Ata. Introduction to Phytocoenology 234 pp.

Chan, E.C.S., Basavanand, P., Liivak, T. (1970). The growth inhibition of *Azotobacter Chroococcum* by *Pseudomonas* sp. Can. J. Microbiol. 16, 9-16.

Cook, M.T. (1921), Wilting caused by walnut trees. Phytopathol. 11, 346.

Corcoran, M.R., Geissman, T.A., Phinney, B.O. (1972). Tannins as gibberellin antagonists. Plant Physiol. 49, 323-330.

Curtis, J.T., Cottam, G. (1950). Antibiotic and auto-toxic effects in prairie sunflower. Bull. Torrey Bot. Club 77, 187-191.

DeCandolle, M.A.P. (1832). "Physiologie Vegetale" Vol III Becht Jeune, Lib. Fac. Med. Paris.

del Moral, R., Cates, R.G. (1971). Allelopathic potential of the dominant vegetation of Western Washington. Ecology 52, 1030-1037.

del Moral, R., Muller, C.H. (1970). The allelopathic effects of *Eucalyptus camaldulensis*. Amer. Midl. Natur. 83, 254-282.

Elkan, G.H. (1961). A nodulation-inhibiting root excretion from a non-nodulating soybean strain. Can. J. Microbiol. 7, 851-856.

Elmer, O.H. (1923). Growth inhibition of potato sprouts by the volatile products of apples. Science 75, 193.

Fenical, W. (1975). Halogenation in the Rhodophyta-A review. J. Phycol. 11, 245-265.

Fisher, R.F., Woods, R.A., Glavicic, M.R. (1978). Allelopathic effects of goldenrod and aster on young sugar maple. Can. J. Forest Res. 8, 1-9.

Fraenkel, G.S. (1959). The raison d'etre of secondary plant substances. Science 129, 1466-1470.

Gabriel, W.J. (1975). Allelopathic effects of black walnut on white birches. J. Forest (Washington) 73, 234-237.

Gaidamak, V.M. (1971). Biologically active substances in nutrient solutions after cucumbers and tomatoes were grown on pure and multiple used broken brick. In Physiological-biochemical basis of plant interactions in phytocenoses (A.M. Grodzinski ed) Vol 2 pp 56-60 Naukova, Kiev.

Glass, A.D.M. (1973). Influence of phenolic acids on ion uptake I. Inhibition of phosphate uptake. Plant Physiol. 51, 1037-1041.

Glass, A.D.M. (1975). Inhibition of phosphate uptake in barley roots by hydroxy-benzoic acids. Phytochem. 14, 2127-2130.

Glass, A.D.M., Dunlop, J. (1974). Influence of phenolic acids on ion uptake IV. Depolarization of membrane potentials. Plant Physiol. 54, 855-858.

Gliessman, S.R. (1976). Allelopathy in a broad spectrum of environments as illustrated by bracken. J. Linn. Soc. Bot. 73, 95-104.

Green, F.B., Corcoran, M.R. (1975). Inhibitory action of five tannins on growth induction by several gibberellins. Plant Physiol. 56, 801-806.

Gupta, N.N., Houdeshell, J. (1976). A differential-difference equations model of a dynamic aquatic ecosystem. Int. J. Systems Sci. 7, 481-492.

Horsley, S.B. (1977 a). Allelopathic interference among plants II. Physiological modes of action. In Proceedings of the Fourth North American Forest Biology Workshop pp 93-146 (H.E. Wilcox, A.F. Hamer, eds) College of Environmental Science and Forestry, Syracuse, New York.

Horsley, S.B. (1977 b). Allelopathic inhibition of black cherry by fern, grass, goldenrod and aster. Can. J. Forest Res. 7, 205-216.

Hussain, A., Mallik, M.A.B (1972). Study of rhizosphere microflora of berseem (*Triloium alexandrinum* L) and their effect on *Rhizobium trifolii*. J. Sci. 1, 139-145.

Jankay, P., Muller, W.H. (1976). The relationships among umbelliferone, growth and peroxidase levels in cucumber roots. Amer. J. Bot. 63, 126-132.

Keck, R.W., Hodges, T.K. (1973). Membrane permeability in plants: changes induced by host-specific pathotoxins. Phytopathol. 63, 226-230.

Kimmins, J.P. (1975). Review of the ecological effects of herbicide usage in forestry. Environment Canada Forest Service Report BC-X-139.

Koeppe, D.E. (1972). Some reactions of isolated corn mitochondria influenced by juglone. Plant Physiol. 27, 89-94.

Koeppe, D.E., Miller, R.J. (1974). Kaempferol inhibitions of corn mitochondrial phosphorylation. Plant Physiol. 54. 374-378.

Kolesnichenko, M.W., Aleikina, M.M. (1976). The rate of protein biosynthesis and absorption of mineral substances by the roots of oak and ash growing together in a forest. Fiziol. Rast. (Mosc.) 23. 127-131.

Kossanel, J.P., Martin, J., Annelle, P., Peinot, M. Vallet, J.K., Kurnej, K. (1977). Inhibition of growth of young radicles of maize by exudations in culture solutions and extracts of ground roots of *Chenopodium album* L. In interactions of plants and microorganisms in phytocenoses, pp 77-86 (A.M. Grodzinsky, ed.) Naukova Dumka, Kiev.

Kuhn, R., Jerchel, D., Moewus, F., Moeller, E.F. (1943). Über die chemische Natur der Blastokoline und ihre Einwirkung auf Keimende Samen, Pollenkdorner, Hefen, Bakterien, Epithelgewebe und Fibroblasten Naturwissenschaften 31, 468.

Lee, I.K., Monsi, M. (1963). Ecological studies on *Pinus densiflora* forest I. Effects of plant substances on the floristic composition of the undergrowth. Bot. Mag. 76, 400-413.

Leonard, R.T., Hodges, T.K. (1980). The plasma membrane. In The Biochemistry of Plants-A comprehensive treatise. Vol 1 (N.E. Tolbert ed) pp 163-182 Academic Press, New York.

Leuck, E.E., Rice, E.L. (1976). Inhibition of *Rhizobium* and *Azotabacter* by rhizosphere bacteria of *Aristida oligantha*. Bot. Gaz. 137, 160-164.

Lodhi, M.A.K., Nickell, G.L. (1973). Effects of leaf extracts of *Celtis laevigata* on the water content, and carbon dioxide exchange rates of three grass species. Bull. Torrey Bot. Club 100, 159-165.

Lorber, P., Muller, W.H. (1976). Volatile growth inhibitors produced by *Salvia leucophylla:* effects on seedling root tip ultrastructure. Amer. J. Bot. 63, 196-200.

Lyon, T.L., Wilson, J.K. (1921). Liberation of organic matter by roots of growing plants. Cornell Univ. Agr. Exp. Sta. Mem. 40.

Mallik, M.A.B., Hussain, A. (1972). Effect of rhizoshpere microflora of *Melilotus alba* Dear. on *Rhizobium meliloti*. J. Sci. 1, 133-138.

Markova, S.A. (1972). Experimental investigations of the influence of oats on the growth and development of *Erysimum cheiranthoides* L. In Physiological-biochemical basis of plant interactions in phytocenoses Vol 3 pp 66-68 (A.M. Grodzinski ed). Naukova Dumka, Kiev.

McCalla, T.M. Duley, F.L. (1948). Stubble mulch studies. Effect of sweetclover on corn germination. Science 108, 163.

McCalla, T.M., Duley, F.L. (1949). Stubble mulch studies III. Influence of soil microorganisms and crop residues on the germination, growth and direction of root growth of corn seeds. Soil Sci. Soc. Amer. Proc. 14, 196-199.

Minar, J. (1974). The effect of couch grass on the growth and mineral uptake of wheat. Folia Fac. Sci. Nat. Univ. Purkynianae Brun. 15, 1-84.

Molisch, H. (1937). "Der Einfluss einer Pflanze auf die andere-Allelopathic". Fischer, Jena.

Muller, C.H. (1970). Phytotoxins as plant habitat variables. Recent Advan. Phytochem. 3, 106-121.

Murphy, T.P. Lean, D.R.S., Nalewajko, C. (1976). Blue-green algae: their excretion of Fe-selective chelators enables them to dominate other algae. Science 192, 900.

Murthy, M.S., Nagodra, T. (1977). Allelopathic effects of *Aristida adscensionis* on *Rhizobium*. J. Appl. Ecol. 14, 279-282.

Murthy, M.S., Ravindra, R. (1974). Inhibition of nodulation of *Indigofera cordifolia* by *Aristida adscensionis*. Oecologia 16, 257-258

Murthy, M.S. Ravindra, R. (1975). Allelopathic effects of *Aristida adscensionis*. Oecologia 18, 243-250.

Neish, A.C. (1964). Major pathways of biosynthesis of phenols. In Biochemistry of Phenolic compounds (J.B. Harbourne ed) pp 295-359. Academic Press, New York.

Neustruyera, S.N., Dobretsova, T.N. (1972). Influence of some summer crops on goosefoot. In Physiological-biochemical basis of plant interactions in phytocenoses. Vol 3 pp 68-73 (A.M. Grodzinski ed) Naukova Dumka, Kiev.

Olsen, R.A. (1975). Triterpeneglycosides as inhibitors of fungal growth and metabolism. Induced leakage of nucleotide materials. Physiol. Plant 33, 75-82.

Overland, L. (1966). The role of allelopathic substances in the "smother crop" barley. Amer. J. Bot. 53, 423-432.

Owens, L.D. (1969). Toxins in plant disease: structure and mode of action. Science 165, 18-25.

Patrick, Z.A. (1955). The peach replant problem in Ontario II. Toxic substances from microbial decomposition products of peach root residues. Can. J. Bot. 33, 461-486.

Patrick, Z.A., Koch, K.W. (1958). Inhibition of respiration, germination and growth by substances arising during the decomposition of certain plant residues in the soil. Can. J. Bot. 36, 621-647.

Perry, G.S. (1932). Some tree antagonisms. Proc. Pennsylvania Acad. Sci. 6, 136-141.

Peterson, E.B. (1965). Inhibition of black spruce primary roots by a water-soluble substance in *Kalmia angustifolia* Forest. Sci. 11, 473-479.

Peterson, G.B. (1972). Determination of the presence, location, and allelopathic effects of substances produced by *Juniperus scopulorum*. Sarg. Diss. Abstr.B 32, 3811-12.

Prutenskaya, N.I. (1974). Peculiarities of interaction between *Sinapis arvensis* L. and cultivated plants. In Physiological-biochemical basis of plant interactions in phytocenoses. Vol 5 pp 66-68 (A.M. Grodzinski ed) Naukova Dumka, Kiev.

Putnam, A.R., Duke, W.B. (1978). Allelopathy in agroecosystems. Annu. Rev. Phytopathol. 16, 431-451.

Rakhteenko, I.N., Kauror, I.A. Minko, I.T. (1973). Effect of water-soluble metabolites from a series of crops on some physiological processes. In physiological-biochemical basis of plant interactions in phytocenoses Vol 4, pp 23-26 (A.M. Grodzinski ed) Naukova Dumka, Kiev.

Rasmussen J.A., Einhellig, F.A. (1975). Non-competitive effects of common milkweed. *Asclepias syriaca* L on germination and growth of sorghum. Amer. Midl. Natur. 94, 478-483.

Ravanel, P., Tissut, M., Douce, R. (1982). Effects of kaempferol on the oxidative properties of intact plant mitochondria. Plant Physiol. 69, 375-378.

Rice, E.L. (1968). Inhibition of nodulation of innoculated legumes by pioneer plant species from abandoned fields. Bull. Torrey Bot. Club 95, 346-358.

Rice, E.L. (1974). Allelopathy. Academic Press, New York.

Rice, E.L. (1979). Allelopathy- an update. Bot. Rev. 45, 15-109.

Rietveld, W.J. (1975). Phytotoxic grass residues reduce germination and initial root growth of Ponderosa pine. USDA Forest Service Res. Paper RM-153.

Robinson, T. (1963). "The Organic Constituents of Higher plants" Burgess, Minneapolis, Minn.

Roshchina, V.D. (1973). Reducing power of woody plant leaf infusions and inhibition of Hill reaction with 2, 6-dichlorophenol by them. In Physiological-biochemical basis of plant interactions in phytocenoses. Vol 4 pp 10-15 (A.M. Grodzinski ed), Naukova Dumka, Kiev.

Schreiber, M.M., Williams, J.L. (1967). Toxicity of root residues of weed grass species. Weeds 15, 80-81.

Schreiner, O., Reed, H.S. (1907). The production of deliterious excretions by roots. Bull. Torrey Bot. Club 34, 279-303.

Schreiner, O., Sullivan, M.X. (1909). Soil fatigue caused by organic compounds. J. Biol. Chem. 6, 39-50.

Stahl, C., Vanderhof, L.N., Siegel, N., Helgelson, J.P. (1973). *Fusarium tricinctum* T-2 toxin inhibits auxin-promoted elongation in soybean hypocotyl. Plant Physiol. 52, 663-666.

Stickney, J.S., Hoy, P.R. (1881). Toxic action of black walnut. Trans. Wis. State Hort. Soc. 11, 166-167.

Strobel, G.A. (1975). A mechanism of disease resistance in plants. Sci. Amer. 232, 80-88.

Swain, T. (1977). Secondary compounds as protective agents. Annu. Rev. Plant Physiol. 28, 479-501.

Szczepanski, A.J. (1977). Allelopathy as a means of biological control of water weeds. Aquatic Bot. 3, 193-197.

Tamura, S., Chang, C., Suzuki A., Kumai, S. (1969). Chemical studies on "clover sickness" Part I. Isolation and structural elucidation of two new isoflavonoids in red clover. Agric. Biol. Chem. 33, 391-397.

Thomas, A.S. (1974). The effect of aqueous extracts of blue spruce leaves on seed germination and seedling growth of several plant species. Phytopathol. 64, 587.

Tubbs, C.H. (1973). Allelopathic relationship between yellow birch and sugar maple seedlings. For. Sci. 19, 139-145.

Tukey, H.B. (1966). Leaching of metabolites from above-ground plant parts and its implications. Bull. Torrey Bot. Club 93, 385-401.

Tukey, H.B. (1969). Implications of allelopathy in agricultural plant science. Bot. Rev. 35, 1-16.

Tukey, H.B. (1971). Leaching of substances from plants. In "Biochemical Interactions among plants". (US Nat. Comm. for IBP, eds) pp 25-32. Nat. Acad. Sci. Washington.

Turner, W.B. (1971). Fungal metabolites. Academic Press, New York.

Van Alfen, N.K. Turner, N.C. (1975). Influence of a *Ceratocystis ulmi* toxin on water relations of elm *Ulmus americana*. Plant Physiol. 55, 312-316.

Van Sumere, C.F., Cottenie, J., de Greef, J., Kint, J. (1971). Biochemical studies in relation to the possible germination regulatory role of naturally occurring coumarius and phenolics. Recent Adv. Phytochem. 4, 165-221.

Weaver, T.W. Klarich, D. (1977). Allelopathic effects of volatile substances from *Artemisia tridentata*. North Amer. Midl. Natur. 97, 508-512.

Whittaker, R.H. (1970). Communities and ecosystems. Macmillan, New York.

Whittaker, R.H. (1971). The chemistry of communities. In "Biochemical Interactions among plants". (US Nat. Comm. for IBP, eds) pp 10-18, Nat. Aca. Sci. Washington.

Whittaker, R.H., Feeny, P.P. (1971). Allelochemics: Chemical Interactions between species. Science 171, 757-770.

Zabyalyendzik, S.F. (1973). Allelopathic interaction of buckwheat and its components through root excretions. Vyestsi Akad. Navuk BSSR Syer Biyal Navuk 5, 31-34.